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## ECOLOGY AND REPRODUCTION OF THE PARTHENOGENETIC LIZARD *CNEMIDOPHORUS UNIPARENS* (TEIIDAE)

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### ABSTRACT

A population of *Cnemidophorus uniparens* was studied in the vicinity of Portal, Cochise County, Arizona, in summer 1977 and 1978. Daily activity was distinctly bimodal with peak activity occurring in the morning. Frequency of tail breakage (a measure of predation) increased with size, but overall tail breakage was low (15.6%). Reproduction began in mid-May and extended to the end of July. Peak reproduction occurred in late June and early July. Clutch size ranged from one to four eggs and was positively correlated with snout-vent length. There was no correlation between individual egg size and body size. Relative clutch mass was low (mean = 14.4%). Mean home range size differed significantly between years and appeared to be related to differences in prey availability between years. Home ranges overlapped and there was no evidence for territoriality or agonistic behavior. Average growth rate was 0.17 mm/day. Growth rate was negatively correlated to snout-vent length. Population size and structure remained relatively constant between years.

## INTRODUCTION

The lizard genus *Cnemidophorus* is large and widespread, ranging from the eastern United States to central Argentina (Peters and Donoso-Barros, 1970). Greatest species diversity within the genus is found in the southwestern United States and northwestern Mexico. The ge-

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nus contains a large number of parthenogenetic species. Of the 16 species inhabiting the southwestern United States nine (58.8%) are all-female parthenospecies (Conant, 1975; Lowe and Wright, 1964; McKinney et al., 1973; Scudday, 1973; Stebbins, 1966).

In recent years an increased interest in the biology of *Cnemidophorus* has resulted in a number of ecological papers dealing with the group. Most of these have been concerned with the biparental species (Parker, 1972; Turner et al., 1969; Vitt and Ohmart, 1977, among others). Less attention has been devoted to the uniparental forms. In the present paper I present data on the ecology, reproduction, and population structure of a uniparental species, *Cnemidophorus uniparens*, from southeastern Arizona.

## MATERIALS AND METHODS

*Cnemidophorus uniparens* was studied during summer (late May to the end of August) 1977 and 1978 at a site approximately 2 km W of the Arizona-New Mexico border along the Portal Road, Cochise County, Arizona. The study site consisted of a pitfall trap grid composed of 100 number 10 cans (155 mm by 170 mm) buried flush with the ground and covered with slightly elevated plywood boards designed to prevent the lizards from escaping and to provide shade during the heat of the day. The cans were set in 10 rows of 10 cans each spaced 10 m apart, so that the grid covered an area of 1 ha. The cans were checked twice daily (ca 1200 h and 1900 h). These times roughly corresponded to the end of morning and evening activity periods for the lizards.

Upon initial capture lizards were given a permanent identification number by toe clipping (Tinkle, 1967). Originally each animal was also marked with a unique color code to allow for easy visual identification from a distance, however, this procedure proved impractical and was soon abandoned due to unequal paint loss, fading, and partial shedding. Later the animals were simply marked with a single dot of paint at the base of the tail. The color of paint was changed weekly. Upon initial capture and all subsequent recaptures the following data were recorded: grid location, snout-vent length (mm), length of tail base (= unregenerated portion of the tail), length of regenerated portion of the tail (mm), weight (measured with a Pesola spring balance to 0.1 g), reproductive condition (determined by palpation), and shedding.

In addition to work on the grid, lizards were sampled weekly from similar habitat near the grid (less than 0.5 km) for detailed information on thermal relations, feeding, and reproduction. Feeding and thermal relations will be reported on in separate papers. Lizards were collected using blowguns constructed of steel or plastic conduit with 12 or 20 gauge shotgun wads as projectiles. This proved to be very effective in collecting *Cnemidophorus* at distances up to 10 m. Immediately upon capture lizards were placed on ice and transported to the laboratory for analysis. In the lab they were measured to the nearest mm and weighed to the nearest 0.01 g on a Mettler top-loading balance. Ovaries were removed and trimmed of superfluous tissue and then weighed to the nearest 0.01 g. Ovarian follicles and corpora lutea were counted and measured in the fresh state to the nearest 0.1 mm with an ocular micrometer attached to a dissecting microscope. Condition of the oviducts was noted and any oviducal eggs removed, weighed, and measured to the nearest 0.1 mm with dial calipers. The liver and fat bodies (if present) were removed and weighed to the nearest 0.01 g.

## DESCRIPTION OF THE STUDY SITE

The study site was located along the Portal Road at the eastern foot of the Chiricahua Mountains in the San Simon Valley at an elevation of approximately 1500 m. The soil on the grid site was sandy with some scattered large rocks. The entire region was dissected by numerous shallow, often poorly defined watercourses (washes). One large wash on the extreme southern portion of the grid drastically affected the density of the vegetation in that region.

Dominant plant species on the grid were mesquite (*Prosopis glanduosa*) and Mormon tea (*Ephedra trifurca*). Subdominants were white thorn acacia (*Acacia albicans*), tarbush (*Flourensia cernua*), snakeweed (*Gutierrezia* sp.), and cowweed (*Boutela* sp.). Total ground cover was sparse, comprising about 15 to 20% except along the southern border in the vicinity of a large wash where *Prosopis glandulosa* formed a dense border. Ground cover on the grid increased slightly (30 to 35%) during late summer due to the appearance of summer annuals after heavy July and August rains.

A dominant aspect of the area in general and the grid in particular was the presence of large earthen mounds produced by the activity of banner-tailed kangaroo rats (*Dipodomys spectabilis*). These mounds were abundant, often exceeding 30/ha. The tunnels within the mounds were a major source of nocturnal retreats and daytime refugia for *Cnemidophorus uniparens* and other lizards on the grid. The site also contained numerous tunnels and burrows of other small heteromyid rodents (*Dipodomys merrami* and *Perognathus* sp.) which were also used as retreats and refugia by the lizards.

Several other species of lizards occurred on the grid with *C. uniparens*. They were *Holbrookia maculata, Phrynosoma cornutum, Phrynosoma modestum, Sceloporus undulatus, Urosaurus ornatus, Uta stansburiana, Crotaphytus wislizenii,* and *Eumeces obsoletus.*

## RESULTS AND DISCUSSION

### Activity

During the course of the study the daily activity pattern of *Cnemidophorus uniparens* was distinctly bimodal with the majority of the activity being concentrated in early morning (from sunrise to about 1130 h) and with a lesser peak in late afternoon (1730 to 1930 h). Morning and afternoon grid capture data show that 75% of all animals were collected during the morning activity period. Virtually no lizards were active during the middle of the day, except on overcast days when midday temperatures were reduced. On such days the bimodal pattern broke down and lizards were active throughout the day. Rainfall depressed activity. Lizards were never active during rain storms and the strength and duration of the storms affected subsequent activity. *Cnemidophorus uniparens* would become active almost immediately after light showers, but heavy rainfall (>3 cm) would often depress activity for as much as 24 to 36 h. The reason for this refractory period remains unclear, however, it may have to do with the difficulty in foraging in rain soaked soil.

Table 1 shows grid capture success during the summers of 1977 and

Table 1.—*Summary of seasonal activity in* Cnemidophorus uniparens *as measured by capture success (average number of animals captured/100 trap days during the time period).*

| Date | 1977 | 1978 |
|------|------|------|
| 16–31 May | No sample | 4.4 |
| 1–15 June | 8.8 | 3.7 |
| 16–30 June | 16.8 | 4.5 |
| 1–15 July | 8.9 | 4.3 |
| 16–31 July | 5.6 | 3.5 |
| 1–15 August | 5.2 | 4.3 |
| 16–31 August | 3.5 | 2.5 |

1978. In 1977 capture success reached a peak in the second half of June and then gradually declined. Even with this decrease, activity remained fairly high until the termination of field work in late August. In 1978 overall capture success was reduced, but activity remained fairly constant throughout the summer, with only a slight decrease in late August.

Daily activity in *C. uniparens* was similar to that reported by other workers for *Cnemidophorus* (for example, Echternacht, 1967; Medica, 1967; Milstead, 1957a; Vitt and Ohmart, 1977). These authors mention the bimodal activity period and cessation of activity with rainfall, but none of them noted a refractory period depending upon amount of rainfall as was seen in *C. uniparens*. Most workers (Christiansen, 1971 and Medica, 1967, among others) have noted a sharp decline in activity of post-reproductive adults, however, prolonged activity after cessation of reproductive activity has been reported for *C. tigris* (Parker, 1972; Vitt and Ohmart, 1977).

## Predation and Tail Breakage

The following species of birds were observed successfully preying on *Cnemidophorus uniparens*: Roadrunners (*Geococcyx californianus*), Burrowing Owls (*Speotyto cunicularia*), and Loggerhead Shrikes (*Lanius ludovicianus*). In addition to these direct observations there are a number of potential avian and reptilian predators on the site. The potential avian predators are Swainson's Hawk (*Buteo swainsoni*), Red-tailed Hawk (*Buteo jamaicensis*), and the American Kestrel (*Falco spaverius*). Potential reptilian predators include *Masticophis flagellum, Salvadora derserticola, Arizona elegans, Rhinocheilus leconti, Lampropeltis getulus,* and juveniles of *Pituophis melanoleucus, Crotalus atrox,* and *Crotalus scutulatus*. With the exceptions of *M. flagellum* and *S. derserticola* (both active diurnal species) most snakes probably encounter whiptails while they are in nocturnal retreats. *Cro-*
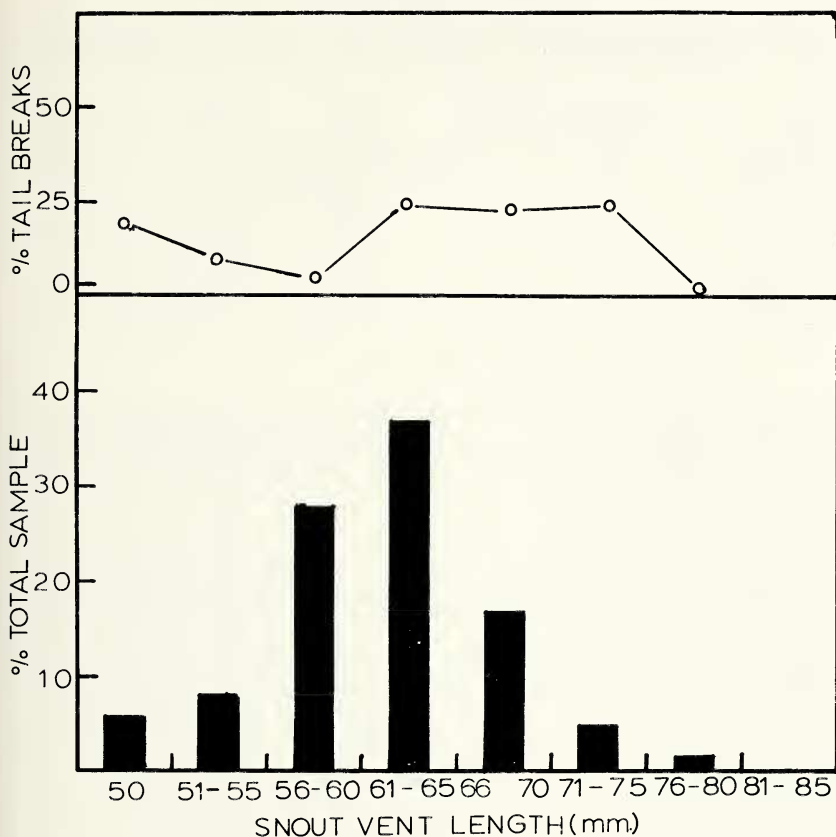
Fig. 1.—Size composition and relative tail breaks by size class for *Cnemidophorus uniparens* (N = 472).

*taphytus wislizenii* also occurs on the grid and the remains of a *C. uniparens* was found in the stomach of a *C. wislizenii*.

Fig. 1 compares population percentage by size class and percent tail breakage within size class. Frequency of tail breakage has been used by many investigators as an indication of relative predation pressure (Tinkle and Ballinger, 1972; Parker and Pianka, 1973; Vitt and Ohmart, 1977) or predation pressure in conjunction with intraspecific aggression (Vitt et al., 1974). The probability of an individual lizard having at some time had an encounter with a predator should increase with increasing age (snout-vent length) and this should then be reflected in increased frequency of tail breakage in the larger size classes. The tail

Table 2.—*Summary of seasonal reproductive cycle in* Cnemidophorus uniparens *by percent of sample possessing the character. Data are pooled for 1977 and 1978.*

| Date | N | Enlarged follicles | Oviducal eggs | Corpora lutea | Enlarged oviducts |
|---|---|---|---|---|---|
| 16–31 May | 6 | 16.6 | 16.6 | 33.3 | 66.6 |
| 1–15 June | 23 | 60.8 | 21.7 | 43.4 | 95.6 |
| 16–30 June | 32 | 62.5 | 21.8 | 40.6 | 96.8 |
| 1–15 July | 34 | 52.9 | 26.4 | 55.8 | 100.0 |
| 16–31 July | 16 | 18.7 | 18.7 | 68.7 | 100.0 |
| 1–15 August | 25 | 0.0 | 0.0 | 24.0 | 0.0 |
| 16–31 August | 9 | 0.0 | 0.0 | 0.0 | 0.0 |

breakage data for *C. uniparens* conforms to the expected prediction. Combined tail breakage for all size classes is 15.6%, and is considerably lower than frequencies reported by Parker (1972) and Vitt and Ohmart (1977) for *Cnemidophorus tigris*. This initially suggests that predation pressure might be lower on *C. uniparens* than on *C. tigris*; however, two other factors, adult body size and demographic structure, might differentially affect tail breakage frequencies in *C. uniparens*. Tail breakage data are actually a measure of unsuccessful predation attempts. A higher success to attack ratio on the part of a predator would potentially reduce the proportion of a population exhibiting regenerated tails. Due to its small size it is probable that *C. uniparens* is less likely to escape a predation event, especially from an avian predator. If this is the case tail breakage frequency is low not because of a reduction in predation but rather to the greater success on the part of the predators. Demographic structure might also affect the frequency of tail breakage. Because frequency of regenerated tails is assumed to be a time related phenomenon, one would expect higher frequencies of tail breakage in populations of long lived organisms. Several studies have shown *C. tigris* to be long lived (McCoy, 1965; Parker, 1972; Turner et al., 1969), whereas the present study suggests that *C. uniparens* is short lived, with few if any animals attaining an age of three years (see section on Population Structure, Density, and Turnover).

### Reproduction and Fat Body Cycles

Females were judged to be reproductively mature if they possessed any of the following: oviducal eggs; corpora lutea; enlarged ovarian follicles; or enlarged, distended oviducts. The smallest mature female collected was 58 mm snout-vent length and the largest immature was 59 mm; however, four other 59 mm animals were mature, having either enlarged ovarian follicles or corpora lutea. All animals over 59 mm

Fig. 2.—Relationship between egg number and snout-vent length for *Cnemidophorus uniparens*. Open circles are oviducal eggs and open squares ovarian follicles near ovulatory size. Numbers in open symbols denote number of individuals sharing a point.

were mature. Minimum size at maturity apparently varies from 58 to 59 mm. Mature females ranged from 58 to 77 mm (mean = 65.5 ± 3.9 mm, N = 145).

The annual reproductive cycle is summarized in Table 2. Samples were not collected before 16 May in either year, but due to the small percentage of animals with either ovarian follicles or oviducal eggs in late May it would seem that little reproductive activity occurs earlier in the year. By early June virtually all animals possessed enlarged oviducts and either actively yolking follicles or oviducal eggs. This heightened reproductive activity continued through the first half of July, rapidly dropped off in the second half of July and stopped by early August. No animals collected in August contained enlarged follicles or oviducal eggs, indicating that reproduction had ceased for the year. Cessation of reproductive activity in late July and early August is further supported by the small or regressing condition of the oviducts of all animals collected in August.

Clutch size was determined from counts of oviducal eggs, enlarged ovarian follicles, or corpora lutea. Clutch size ranged from one to four eggs (mean = 2.77 ± 0.06, N = 105). There was a significant correlation between clutch size and snout-vent length (Fig. 2, $P < 0.001$) with greater than 40% ($r^2 = .44$) of the variation in clutch size being attributable to increase in snout-vent length. The slope of the regression line indicated that an additional egg would be added to the clutch with every 7 mm increase in snout-vent length. *Cnemidophorus uniparens* produced multiple clutches of eggs in a year, as was demon-

strated by the presence of both corpora lutea and ovarian follicles near ovulatory size in several animals. Individual mark-recapture data confirm multiple clutches with females collected while gravid, spent, and gravid again. Time between clutches in these individuals varied from 21 to 28 days. It is probable that most, if not all, females lay two clutches per year and that some could produce three clutches due to the relatively short time between clutches and the extended reproductive season (late May to early August).

Egg size was variable in *C. uniparens*. Mean egg size for 66 shelled oviducal eggs was 13.1 mm ± 1.3 mm by 7.1 mm ± 0.8 mm with a range of 11.5 to 16.4 mm for egg length and 5.7 to 8.2 mm for egg width. Egg weight varied from 0.30 to 0.52 g (mean = 0.38 ± 0.05 g). There was no significant correlation between snout-vent length and either egg size or egg weight.

Relative clutch mass (sensu Vitt and Congdon, 1978) as used here refers to the ratio of total clutch weight of shelled oviducal eggs to total body weight. No attempt was made to determine either dry weight ratios or caloric ratios. Ballinger and Clark (1973) have demonstrated that wet weight ratios are comparable to both dry weight and caloric ratios (but see Vitt and Congdon, 1978). Relative clutch mass was low, ranging from 9.6% to 20.0% (mean = 14.4 ± 0.24). Using the Wilcoxon's two sample test (Sokal and Rohlf, 1969) there was no significant difference in relative clutch mass between 1977 and 1978 samples, between early and late season clutches, or between small (≤65 mm) and large (≥66 mm) animals.

Reproductive potential refers to the total number of eggs produced by an average female during a single breeding season. As a result it is a function of both clutch size and number of clutches. Mean clutch size for *C. uniparens* was 2.77 eggs and lizards laid from two to three clutches per season. Therefore average annual reproductive potential for *C. uniparens* varies from 5.5 to 8.7 eggs.

The importance of fat bodies to lizard reproduction has been experimentally demonstrated by Hahn and Tinkle (1965). No clear picture of fat body cycling was obtained in the present study, but this is probably a function of sampling time, rather than the biology of the animals. Fat bodies were either absent or very small from the initial samples in May through the end of July. In August fat bodies began to appear and became progressively larger until the termination of the study in the end of August. It is probable that by the time sampling was initiated in mid-May the fat body lipids had already been mobilized for reproduction. With the end of the reproductive season in late July, energy that would earlier have been allocated for reproduction could be shunted into fat body storage, presumably to be used both as a source of

energy during brumation and to initiate vitellogenesis in the following spring.

## Home Range

Home range size in *Cnemidophorus uniparens* was detemined by the convex polygon method. Only animals with five or more captures, with none of the capture points occurring on the border of the grid were used in the analysis. These restrictions were placed on the analysis to prevent unrealistically small home ranges being generated either from animals with too few captures, or from lizards that had some or most of their home ranges outside the confines of the study grid. It was assumed that an animal that was never captured along the margin of the grid had its total home range within the study site. A total of 47 animals met these requirements.

Much debate has arisen concerning both the methods utilized in determining home range size and the meaning of home range data (Turner, 1971; Wieazlowska, 1975; Waldschmidt, 1979, among others). I have chosen the convex polygon method rather than statistical probabilistic methods such as the recapture radii method (Tinkle and Woodward, 1967) or the probability ellipse method (Jennrich and Turner, 1969), because it measures home range only in regions where the animals have been captured, rather than measuring the home range as some probability function. Methods such as recapture radii and probability ellipse consistently over-estimate home ranges compared to the convex polygon method (Wieazlowska, 1975; Waldschmidt, 1979).

Size of the home range was not significantly correlated with either number of captures ($r = .28$, $P < 0.1$) or with snout-vent length of the animals ($r = .12$, $P > 0.1$). Combined size of home range for both years varied from a minimum of 120 m² to a maximum of 2386 m² (mean = 728 m² ± 77 m²). For 1977 home range varied from 120 m² to 2386 m² (mean = 815 m² ± 88 m², N = 39). In 1978 home range size varied from 240 m² to 746 m² (mean = 417 m² ± 62 m², N = 8). The difference between mean home range size in the two years is highly significant (*t*-test, $P < 0.001$). This difference in home range size between 1977 and 1978 is probably a function of different invertebrate prey availability during the two summers. A correlation has been shown between increased rainfall in desert regions and increased primary productivity, which in turn produces higher densities of invertebrate herbivores and detritivores (Dunham, 1978; Whitford and Creusere, 1977). Summer 1977 was preceded by a year of average rainfall, whereas heavy rains preceded summer 1978, greatly increasing the density of spring annuals and their invertebrate herbivores. Apparently *C. uniparens* responded to this increased prey availability

by reducing average size of home range. In a widely foraging species such as *C. uniparens* home range size should be inversely related to prey density, with animals having to forage further during times of prey paucity than during times of prey abundance. The upper limit on home range size is set by the trade-off between energy expended in foraging and energy gained from increased foraging area (home range).

*Cnemidophorus uniparens* exhibited no signs of territoriality. Home ranges greatly overlapped and in some cases the home range of one individual was completely encompassed by that of another. I did not observe any sign of agonistic behavior among the lizards, even when they were close to each other. It was not unusual to find two individuals foraging within 20 to 30 cm of each other, or to find two or more individuals taking refuge under the same shrub. As many as four animals have been found in the same pit trap, resting on top of each other with no sign of aggression. This lack of aggression between individuals would be predicted from the parthenogenetic mode of reproduction where all animals within a population should theoretically share the same genotype. Congdon et al. (1978) have also reported a lack of agonistic behavior in the uniparental *Cnemidophorus* that they studied. However, this appears to not always be the case. Milstead (1957*b*) found *C. tesselatus* to exhibit some intraspecific aggression and Cole and Townsend (1977) alluded to possible intraspecific aggression in various uniparental species under laboratory conditions. In addition Congdon et al. (1978) referred to intraspecific aggression in the "unisexual *C. perplexus*" as reported by Milstead (1957*b*), however, in a reassessment of the nomenclature used in his 1957 study Milstead (1965) equated *C. perplexus* with *C. inornatus,* a biparental species.

The occurrence of agonistic behavior in some populations of uniparentals is puzzling considering the supposed genetic make-up of the populations. It would be interesting to analyze the genetic make-up of those populations that exhibit agonistic behavior to determine if they really are genetically homogeneous.

### Growth and Tail Regeneration

Growth rates were determined for all lizards exhibiting growth with a minimum of 10 days between captures. Using these criteria growth rates could be calculated for 80 *Cnemidophorus uniparens*.

Growth rates were variable, ranging from 0.03 mm/day to 0.6 mm/day, with an average growth rate of 0.17 mm/day for both years. There was no significant difference in mean growth rates between years (1977, mean = 0.171 mm ± 0.017 mm, and 1978, mean = 0.176 mm ± 0.023 mm). Dunham (1978) noted a direct correlation between prey availability and rate of growth in *Sceloporus merriami,* with growth
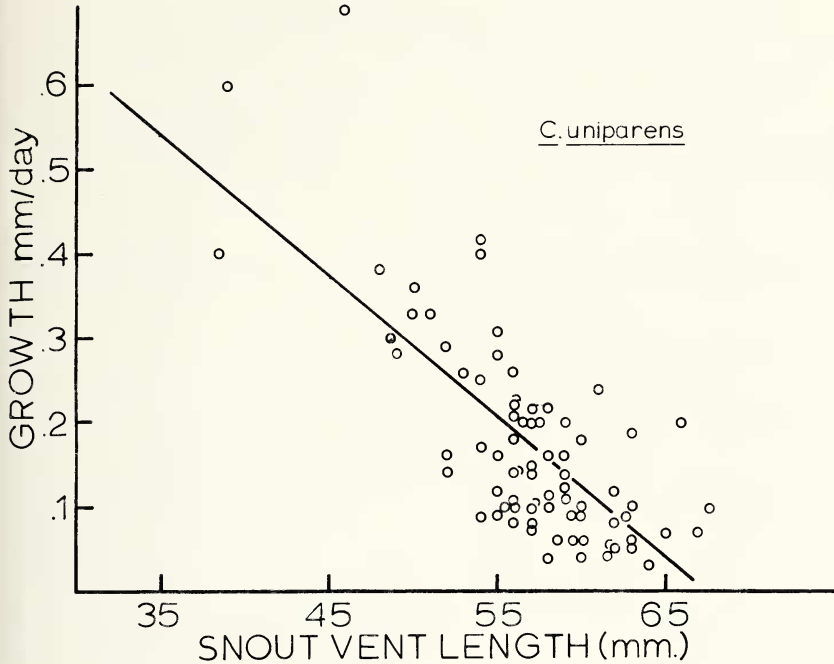
Fig. 3.—Relationship between growth rate and snout-vent size in *Cnemidophorus uniparens*.

rate being greater in years of high prey availability. However, he also noted that prey capture success was positively correlated with prey availability. In *C. uniparens* differences in prey availability between years did not influence volume of prey consumed (Hulse, personal observation). As a result of this growth rates remained unchanged even in years of varying prey availability.

Growth rate was negatively correlated with snout-vent length (Fig. 3, r = .7, $P < 0.001$), with animals below 60 mm having significantly higher growth rates than those greater than 60 mm. Highest growth rates were found among hatchlings between 32 and 50 mm (mean = 0.46 ± 0.07 mm/day, N = 6). Lowest growth rates were found for reproductively mature animals (mean = 0.098 ± 0.01 mm/day).

Growth of regenerated tails was rapid with rates ranging from 0.16 to 1.6 mm/day (mean = 0.757 ± 0.16, N = 8). There was a significant negative correlation between rate of regenerated tail and length of tail
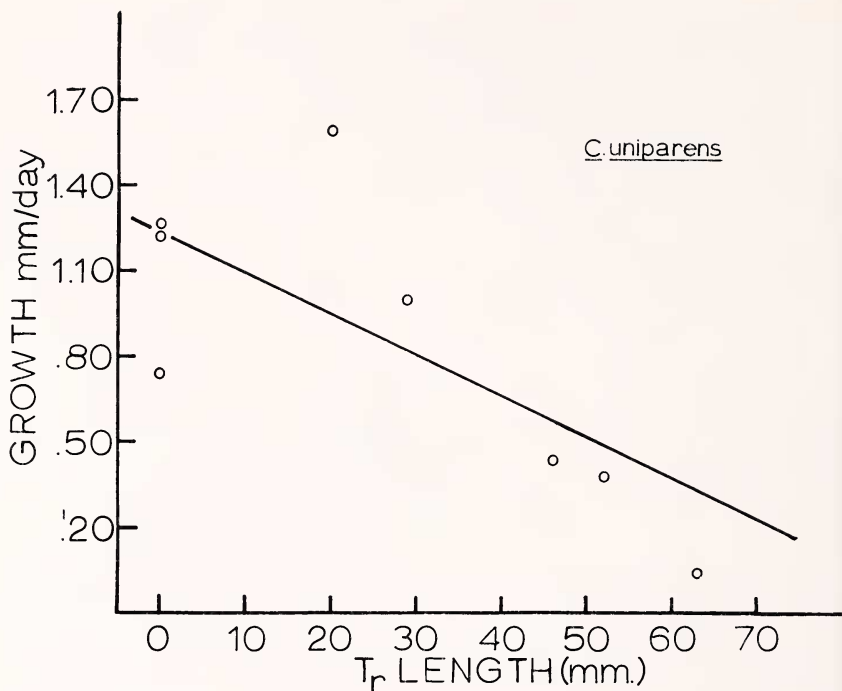
Fig. 4.—Relationship between growth of regenerated tail and length of tail already regenerated.

already regenerated (Fig. 4, r = .72, $P < 0.05$), indicating that initial growth is very rapid, but quickly tapers off as regeneration proceeds to maximum tail length.

The only other work on growth rates in *Cnemidophorus* is that of Fitch (1958) for *C. sexlineatus*. He found growth rates of approximately 0.5 mm/day for hatchling lizards from 32 to 52 mm. Larger animals grew at reduced rates, 0.22 mm/day (55–68 mm) and 0.18 mm/day (66–73 mm). His results are very similar to mine.

Energy assimilated by animals may be used for growth, maintenance, and reproduction. Apportionment of energy for growth and reproduction should be a trade-off between increased fitness through increased body size and increased reproductive effort. A sharp decline in growth rate of *C. uniparens* occurs with attainment of reproductive size, at which point most energy above the maintenance level is shunted into reproduction. One would predict that the majority of growth

Table 3.—*Population density estimates for* Cnemidophorus uniparens.

| Year | Total marked | Total with two or more captures | Lincoln-Peterson estimate |
|------|--------------|--------------------------------|---------------------------|
| 1977 | 135 | 98 | 103 ± 6 |
| 1978 | 138 | 82 | 78 ± 12 |

in adults should occur after the reproductive season, unfortunately my data are not extensive enough to show whether or not this occurs.

## Population Density, Structure, and Turnover

Population size was estimated by computing Lincoln-Peterson Indices during the middle of the collecting season (mid-June to mid-July), with a two week precensus period and a 2 week census period. Results of these estimates are listed in Table 3. Because estimates were made during mid-season, the population densities exclude hatchlings. The differences in estimates for *C. uniparens* in 1977 and 1978 are not significant. Total number of adults marked (135 and 138) was nearly identical for the 2 years. The difference between total animals marked and the density estimates is probably a function of single captures of individuals along the margin of the grid. For these animals, it may be assumed that the majority of their home range occurs off of the site and that their capture along the margin was a rare event. The number of animals captured two or more times was 98 and 82 for 1977 and 1978, respectively. These numbers are very similar to the Lincoln-Petersen Indices for those years.

Few studies have examined population densities in *Cnemidophorus*. Fitch (1958) reported densities of *C. sexlineatus* that varied from 96 to 172 animals per hectare over a 4-year period in Kansas. Clark (1976) reported population estimates ranging from 15 to 24/ha in an east-central Texas population of *C. sexlineatus*. Mitchell (1979) found *C. uniparens* to be the most abundant of four species of *Cnemidophorus* that he studied in southeastern Arizona, with a minimum density of 18 animals per hectare. Fitch's densities are most likely over-estimates caused by the long and narrow (7.6 m by 304 m) shape of his study area. The estimate of Mitchell is an underestimate because he determined densities simply by line transect counts. He suggests that actual densities are between two and three times his estimates.

Fig. 5 illustrates population structure by size class for *C. uniparens*. The data are pooled for both years, because no significant differences were noted between years. Population size structure changes with time, with the smaller size classes becoming less common as the sea-
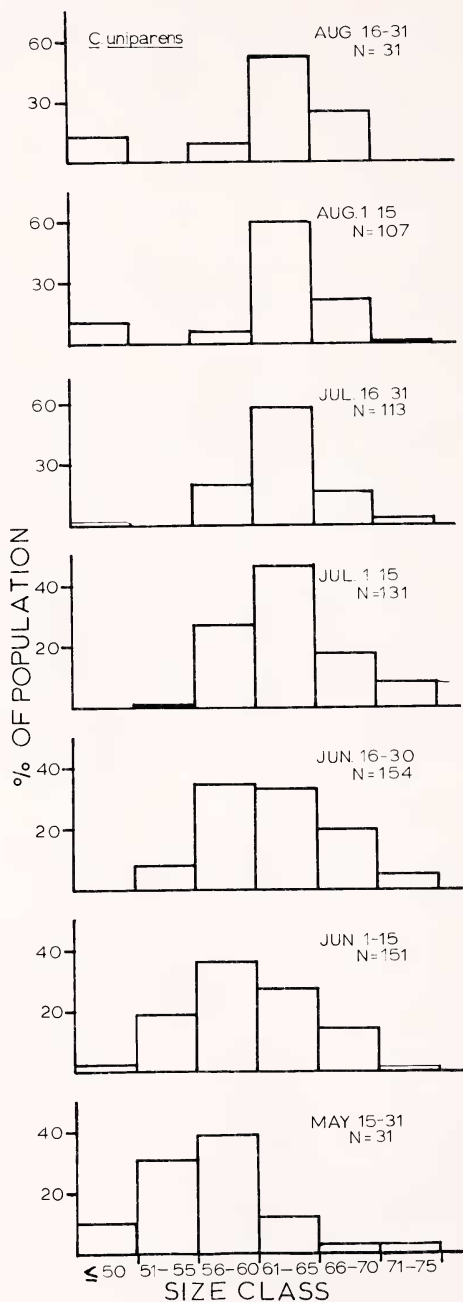
Fig. 5.—Change in size structure of *Cnemidophorus uniparens* population with time.

son progresses, until the end of the sampling periods when all individuals were either large adults or hatchlings. The data strongly suggest an annual cycle with hatchlings appearing from mid-July through August (possibly into September), rapid growth of the hatchlings in the autumn and following spring and the achievement of maturity by the beginning of the reproductive season in late May. Less than 10% of the population consisted of the larger size classes in late May, further supporting the presence of an annual turnover. Of the 135 individuals marked during the 1977 field season, only 12 (8.8%) were recaptured the following year, suggesting a very high mortality over winter in the second year animals. This assumes that all animals marked remain on the study site. There is some evidence that certain individuals have a mobile home range and that the range changes from year to year. Three of the 12 animals recaptured in 1978 had shifted home ranges to other areas of the site, in addition a few marked specimens from 1977 were collected off the site in 1978. This mobility should however, have little effect on the over-all proportion of size classes, assuming that in a homogeneous environment, such as that found in the vicinity of the study area, movement of home ranges is a random event.

## ACKNOWLEDGMENTS

## LITERATURE CITED

BALLINGER, R. E., AND D. R. CLARK, JR. 1973. Energy content of lizard eggs and the measurement of reproductive effort. J. Herpetol., 7:129–132.

CHRISTIANSEN, J. L. 1971. Reproduction in *Cnemidophorus inornatus* and *Cnemidophorus neomexicanus* (Sauria, Teiidae) in northern New Mexico. Amer. Mus. Novitates, 2442:1–48.

CLARK, D. R., JR. 1976. Ecological observations on a Texas population of six-lined racerunner, *Cnemidophorus sexlineatus* (Reptilia, Lacertilia, Teiidae). J. Herpetol., 10:133–138.

COLE, C. J., AND C. R. TOWNSEND. 1977. Parthenogenetic reptiles: New subjects for laboratory research. Experientia, 33:285–289.

CONANT, R. 1975. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin Co., Boston, 429 pp.

CONGDON, J. D., L. J. VITT, AND N. D. HADLEY. 1978. Parental investment: comparative reproductive energetics in bisexual and unisexual lizards, genus *Cnemidophorus*. Amer. Nat., 112:509–521.

DUNHAM, A. E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. Ecology, 59:770–778.

ECHTERNACHT, A. C. 1967. Ecological relationships of two species of lizard genus *Cnemidophorus* in the Santa Rita Mountains of Arizona. Amer. Midland Nat., 78:448–459.

FITCH, H. S. 1958. Natural history of the six-lined racerunner (*Cnemidophorus sexlineatus*). Univ. Kansas Publ., Mus. Nat. Hist., 11:1–62.

HAHN, W. E., AND D. W. TINKLE. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. J. Exp. Zool., 158:79–85.

JENNRICH, R. I., AND F. B. TURNER. 1969. Measurement of non-circular home range. J. Theor. Biol., 22:227–237.

LOWE, C. H., AND J. W. WRIGHT. 1964. Species of the *Cnemidophorus exsanguis* subgroup of whiptail lizards. J. Arizona Acad. Sci., 3:78–80.

MCKINNEY, C. O., F. R. KAY, AND R. A. ANDERSON. 1973. A new all female species of the genus *Cnemidophorus*. Herpetologica, 29:361–365.

MCCOY, C. J. 1965. Life history and ecology of *Cnemidophorus tigris septentrionalis*. PhD dissert., Univ. Colorado, Boulder, 167 pp.

MEDICA, P. A. 1967. Food habits, habitat preference, reproduction, and diurnal activity in four sympatric species of whiptail lizards (*Cnemidophorus*) in south central New Mexico. Bull. Southern California Acad. Sci., 66:251–276.

MILSTEAD, W. W. 1957*a*. Observations on the natural history of four species of whiptail lizards, *Cnemidophorus* (Sauria, Teiidae) in Trans-Pecos Texas. Southwestern Nat., 2:105–121.

———. 1957*b*. Some aspects of competition in natural populations of whiptail lizards (genus *Cnemidophorus*). Texas J. Sci., 9:410–447.

———. 1965. Changes in competing populations of whiptail lizards (*Cnemidophorus*) in southwestern Texas. Amer. Midland Nat., 73:75–80.

MITCHELL, J. C. 1979. Ecology of southeastern Arizona whiptail lizards (*Cnemidophorus*, Teiidae): population density, resource partitioning, and niche overlap. Canadian J. Zool., 57:1487–1499.

PARKER, W. S. 1972. Ecological study of the western whiptail lizard, *Cnemidophorus tigris gracilis* in Arizona. Herpetologica, 28:360–369.

PARKER, W. S., AND E. R. PIANKA. 1973. Notes on the ecology of the iguanid lizard, *Sceloporus magister*. Herpetologica, 29:143–152.

PETERS, J. S., AND R. DONOSO-BARROS. 1970. Catalogue of Neotropical squamata Part II. Lizards and Amphisnaenians. Smithsonian Institution Press, Washington, D.C., 293 pp.

SCUDDAY, J. F. 1973. A new species of lizard of the *Cnemidophorus tesselatus* group from Texas. J. Herpetol., 7:363–372.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, 776 pp.

STEBBINS, R. C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston, 279 pp.

TINKLE, D. W. 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. Misc. Publ. Mus. Zool., Univ. Michigan, 132:1–182.

TINKLE, D. W., AND R. E. BALLINGER. 1972. *Sceloporus undulatus*: a study of intraspecific comparative demography of a lizard. Ecology, 53:570–584.

TINKLE, D. W., AND D. WOODWARD. 1967. Relative movement of lizards in natural populations as determined from recapture radii. Ecology, 48:166–168.

TURNER, F. B. 1971. Estimating lizard home ranges. Herpetol. Rev., 3:77.

TURNER, F. B., P. A. MEDICA, J. R. LANNOM, AND G. A. HODDENBACH. 1969. A demographic analysis of fenced populations of the whiptail lizard, *Cnemidophorus tigris*, in southern Nevada. Southwestern Nat., 14:189–201.

VITT, L. J., AND J. D. CONGDON. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. Amer. Nat., 112:595–608.

VITT, L. J., J. D. CONGDON, A. C. HULSE, AND J. E. PLATZ. 1974. Territorial aggressive encounters and tail breaks in the lizard *Sceloporus magister*. Copeia, 1974:990–993.

VITT, L. J., AND R. D. OHMART. 1977. Ecology and reproduction of lower Colorado River lizards: II. *Cnemidophorus tigris* (Teiidae) with comparisons. Herpetologica, 33:223–234.

WALDSCHMIDT, S. R. 1979. The effect of statistically based models on home range size estimates in *Uta stansburiana*. Amer. Midland Nat., 101:236–240.

WHITFORD, W. G., AND F. M. CREUSERE. 1977. Seasonal and yearly fluctuations in Chihuahuan desert lizard communities. Herpetologica, 33:54–65.

WIEAZLOWSKA, T. 1975. Review of methods of estimating the parameters of home range of small forest rodents from the aspects of sample size. Acta Theriol., 20:3–22.